

# Impulsiveness without discounting: the ecological rationality hypothesis

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Observed animal impulsiveness challenges ideas from foraging theory about the fitness value of food rewards, and may play a role in important behavioural phenomena such as cooperation and addiction. Behavioural ecologists usually invoke temporal discounting to explain the evolution of animal impulsiveness. According to the discounting hypothesis, delay reduces the fitness value of the delayed food. We develop an alternative model for the evolution of impulsiveness that does not require discounting. We show that impulsive or short-sighted rules can maximize long-term rates of food intake. The advantages of impulsive rules come from two sources. First, naturally occurring choices have a foreground–background structure that reduces the long-term cost of impulsiveness. Second, impulsive rules have a discrimination advantage because they tend to compare smaller quantities. Discounting contributes little to this result. Although we find that impulsive rules are optimal in a simple foreground–background choice situation in the absence of discounting, in contrast we do not find comparable impulsiveness in binary choice situations even when there is strong discounting.

**Keywords:** impulsivity; discounting; choice; foraging

## 1. INTRODUCTION

In a classic study, McDiarmid & Rilling (1965) offered pigeons a choice between two schedules of food delivery. One option delivered two units of food in 2 min, whereas the other delivered four units of food in 2 min. The low-rate option consisted of one food delivery after 6 s and another after 114 s; the high-rate option consisted of four food deliveries starting after a delay of 24 s, followed by three more deliveries, one every 6 s. McDiarmid and Rilling's pigeons preferred the low-rate option, even though the high-rate option provided twice as much food. Several investigators have documented the powerful effect of immediacy on choice (e.g. Fantino 1969; Rachlin & Green 1972; Ainslie 1974; Mazur & Logue 1978; Green *et al.* 1981; Fantino & Davison 1983; Mazur 1987; Green & Myerson 1996), and results such as McDiarmid & Rilling's are typical. This impulsiveness presents an evolutionary puzzle: how can natural selection favour choice mechanisms that produce less food?

Students of feeding behaviour usually invoke economic discounting to explain impulsiveness. According to the discounting hypothesis, delay fundamentally reduces the value of benefits. Discounting is probably an important and pervasive economic force that has its roots in collection risk (delayed benefits are less likely to be realized) and lost opportunity costs (delayed benefits cannot be put to use until they are realized). On the basis of our view of plausible levels of collection risk and lost opportunity costs, we argue that discount rates should be relatively small. Discounting could plausibly explain how food today is better

than food next week, or perhaps even food tomorrow, but it seems unlikely that these forces could account for a situation where waiting an additional 18 s would produce twice as much food!

We propose that impulsive choice rules have evolved because they produce high long-term gains in natural-choice situations. This idea emerged from a comparison of two experimental situations: the self-control and patch situations (figure 1). The self-control situation offers a straightforward choice between a small immediate alternative and a large delayed alternative. Self-control-based studies show powerful effects of immediacy and are the main evidence for animal impulsiveness (e.g. Rachlin & Green 1972; Mazur 1987; Bateson & Kacelnik 1996). In the patch situation the subject chooses between a larger amount in a longer time and a smaller amount in a shorter time by choosing whether to stay or leave. Experimental and theoretical evidence indicates that impulsive choice rules can achieve high intake rates in the patch situation (Stephens & Anderson 2001; Stephens 2002), suggesting that impulsive choice rules may have evolved not because immediate outcomes have high fitness value but because impulsive rules achieve high long-term gains in natural-choice situations such as the patch situation in figure 1*b*.

### (a) Choice in 'standard form'

In developing these ideas, we need a framework that puts the self-control and patch situations in a standard form. Our standardization scheme represents alternatives as 'paths' beginning at the choice point and terminating at a second (identical) choice point (figure 2). Figure 1*c,d* shows the self-control and patch situation in this standard form. We use a prime to distinguish one alternative from

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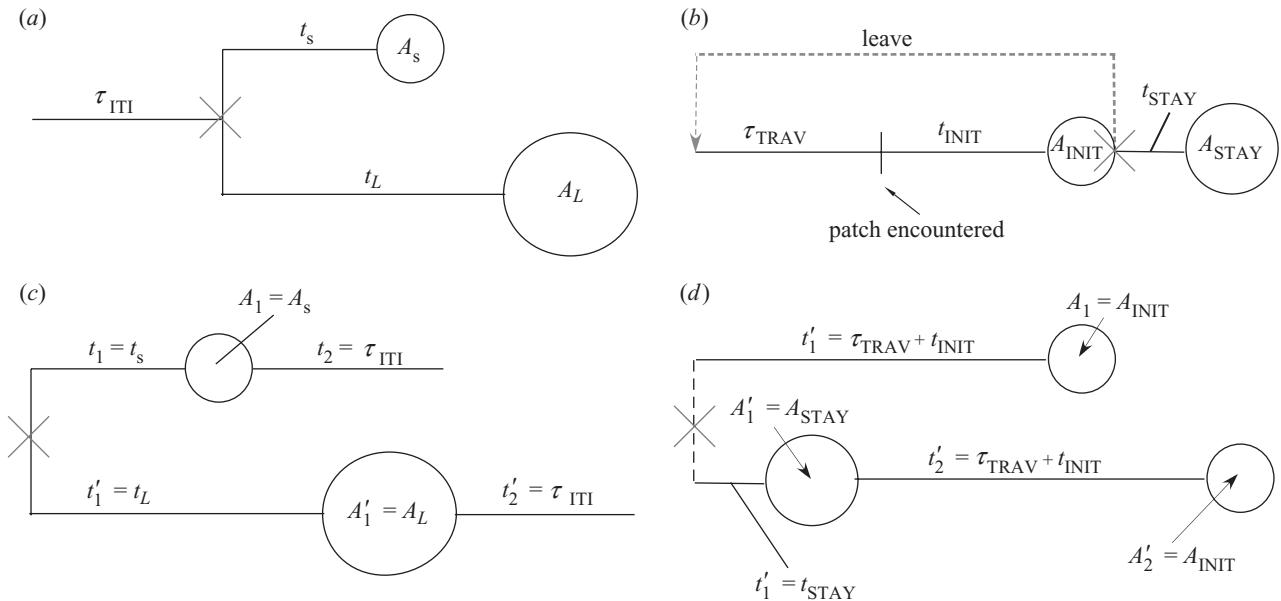


Figure 1. Diagrams showing two choice situations and their representations in standard form. (a) The self-control situation. The animal waits for  $\tau_{\text{ITI}}$  and then faces a choice between a small immediate option ( $A_s$  delivered after  $t_s$  seconds), and a large delayed option ( $A_L$  delivered after  $t_L$ ). (b) The patch situation. The animal waits (travels) for  $\tau_{\text{TRAV}}$  seconds and encounters a patch; after ‘entering’ the patch it waits to  $t_{\text{INIT}}$  seconds after which amount  $A_{\text{INIT}}$  is delivered. The animal must then choose between leaving the patch (initiating a new travel time), or staying. If the animal stays, it waits a further  $t_{\text{STAY}}$  seconds and then obtains amount  $A_{\text{STAY}}$ . (c) The self-control situation in standard form (see figure 2). The same pair of options as in (a) represented in a standardized choice-point-to-choice-point diagram. (d) The patch situation in standard form.

the other (figure 2). For example, the vector  $(t_1, A_1, t_2, A_2)$  represents the first delay, first amount, second delay and second amount associated with the first alternative, while  $(t'_1, A'_1, t'_2, A'_2)$  give the corresponding quantities for the other alternative.

We use two hypothetical choice rules to formalize the difference between far-sighted and impulsive choice. A far-sighted animal would choose the unprimed alternative if

$$(A_1 + A_2)/(t_1 + t_2) > (A'_1 + A'_2)/(t'_1 + t'_2). \quad (1.1)$$

This *long-term rule* simply evaluates the long-term intake rate associated with each alternative. By contrast, an animal following the impulsive *short-term rule* would choose the unprimed alternative if

$$A_1/t_1 > A'_1/t'_1. \quad (1.2)$$

These rules caricature the difference between long- and short-term rules; they capture many properties of this more general comparison in an algebraically simple way.

The long- and short-term rules disagree in the self-control situation. An animal implementing the short-term rule will select the small-immediate option even when this commits it to a long post feeding delay that lowers its overall intake rate. Broadly speaking, however, the empirical evidence suggests that this is how subjects behave in the self-control situation (e.g. Green *et al.* 1981; Bateson & Kacelnik 1996).

By contrast, the long- and short-term rules always agree in the patch situation, because of the patch situation’s special structure. The second food delivery in the stay alternative is identical to the first and only delivery of the leave alternative (that is,  $A'_2 = A_1$  and  $t'_2 = t_1$ ; see figure

1b,d), so for the patch situation the long-term rule is

$$A_1/t_1 > (A'_1 + A_1)/(t'_1 + t_1), \quad (1.3)$$

while the short-term rule is

$$A_1/t_1 > A'_1/t'_1. \quad (1.4)$$

One can easily confirm that these two expressions are algebraically equivalent.

This simple patch situation eliminates the long-term cost of impulsive choice, putting impulsive short-term comparisons on an equal footing with long-term comparisons. If we add imperfect discrimination to the mix, we can tip the balance in favour of impulsive rules. Consider a self-control situation where both alternatives offer the same amount of food. Obviously, the subject’s problem is to pick the option that leads to food in the shortest time. A long-term rule would compare  $t_1 + k$  and  $t'_1 + k$  (since  $t_2 = t'_2 = k$  the common inter-trial interval), while a short-term rule would simply compare  $t_1$  and  $t'_1$ . In a world of error-free discrimination these rules agree precisely, but in a world of imperfect discrimination, elementary psychophysics (i.e. Weber’s Law) tells us that judging the difference between  $t_1 + k$  and  $t'_1 + k$  will be more difficult than judging the difference between  $t_1$  and  $t'_1$  (Gescheider 1985). In this case, an animal using the impulsive, short-term rule will make fewer errors and will achieve a higher long-term intake rate than an animal comparing the long-term rates.

### **(b) Ecological rationality hypothesis**

The ecological rationality hypothesis claims that impulsive choice rules have evolved for two reasons: (i) natural choice situations have a patch-like structure that reduces the long-term cost of impulsive rules; (ii) impulsive

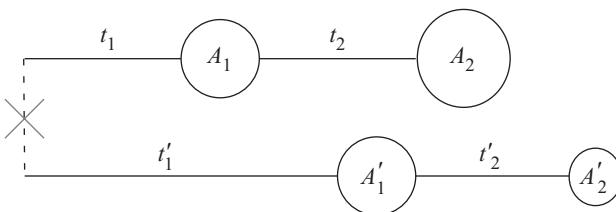


Figure 2. A generic pair of options shown in our standardized notation. This notation imagines options as paths from one choice point to the next identical choice point. The unprimed option yields a delay to  $t_1$ , followed by amount  $A_1$ , followed a second delay of  $t_2$ , followed by amount  $A_2$ . To represent several possibilities  $t_2$  and  $A_2$  may be zero. We use a prime symbol to denote the corresponding quantities for the other option.

choice rules have a discrimination advantage over farsighted rules. While this explanation does not require economic discounting, neither does it exclude discounting. This paper explores the ecological rationality hypothesis by considering how choice situation (e.g. patch versus self-control), discrimination accuracy and discounting influence optimal choice rules. The phrase ‘ecological rationality’ is from Todd & Gigerenzer (2000).

## 2. METHODS

Using numerical optimization, we ask how a rule that evolved to acquire resources in a self-control situation should differ from a rule that evolved to acquire resources in a patch situation. We consider rules that generalize the comparisons of the long- and short-term models. Specifically, our rule favours the unprimed option when

$$(A_1 + \rho_A A_2)/(t_1 + \rho_t t_2) > (A'_1 + \rho_A A'_2)/(t'_1 + \rho_t t'_2), \quad (2.1)$$

where  $\rho_t$  and  $\rho_A$  determine the form of the rule. The  $\rho$  terms give the relative weight placed on future food deliveries, with  $\rho_A$  specifying the weight placed on future amounts, and  $\rho_t$  representing the weight placed on future delays. If both  $\rho$  values are zero, the rule places no weight on the second food delivery, and we have the short-term rule. If both  $\rho$  values equal one, the rule places equal weight on the first and second food deliveries, so we have the long-term rule. If both  $\rho$  values are greater than one, we have a rule that places more weight on future food deliveries.

To determine the fitness of a  $\rho$ -based rule we must translate inequality (equation (2.1)) into a probability of choice. Let  $p$  be the probability that the rule will choose the unprimed option when a choice is presented. We assume that

$$p = \frac{x^D}{1 + x^D}, \text{ where } x = \left( \frac{A_1 + \rho_A A_2}{A'_1 + \rho_A A'_2} \right) \left( \frac{t'_1 + \rho_t t'_2}{t_1 + \rho_t t_2} \right). \quad (2.2)$$

The function  $x^D / (1 + x^D)$  is sigmoid function of  $x$  with an inflection point at  $x = 1$ . We take  $x$  to be the ratio formed from the left and right-hand sides of expression (2.1), so that if these two scores are equal the rule judges the two options to be equivalent ( $x = 1$  implies  $p = 1/2$ ). When  $x$  increases above one, the rule judges the unprimed option to be superior and  $p$  will increase above 1/2, eventually approaching 1 if  $x$  continues to increase. If  $x$  is less than one, the opposite applies, with  $p$  eventually decreasing to zero. The parameter  $D$  measures discrimination accuracy: when  $D$  is large the function  $x^D / (1 + x^D)$  approaches a step function, so a

small difference can create a dramatic change in behaviour; when  $D$  is small, the function has a shallower slope.

### (a) Fitness functions, environment and numerical technique

In our first study we assume a fitness criterion without discounting based on long-term rate, as assumed in traditional foraging theory (Stephens & Krebs 1986),

$$W_\theta(p) = \frac{p(A_1 + A_2) + (1 - p)(A'_1 + A'_2)}{p(t_1 + t_2) + (1 - p)(t'_1 + t'_2)}, \quad (2.3)$$

where we use  $\theta$  to represent the pair of options for which fitness is evaluated; for example,  $\theta = \{t_1, A_1, t_2, A_2, t'_1, A'_1, t'_2, A'_2\}$ . In our second study, we allow discounting at rate  $\lambda$ , which gives

$$\begin{aligned} W_\theta(p) \\ = \frac{p(A_1 e^{-\lambda t_1} + A_2 e^{-\lambda(t_1+t_2)}) + (1 - p)(A'_1 e^{-\lambda t_1} + A'_2 e^{-\lambda(t'_1+t'_2)})}{1 - p e^{-\lambda(t_1+t_2)} - (1 - p)e^{-\lambda(t'_1+t'_2)}} \end{aligned} \quad (2.4)$$

(Stephens 2002; electronic Appendix A). Since our rule specifies the probability of choice  $p$  for a given pair of options, we can calculate the fitness associated with a particular rule for a given pair of options using equation (2.3) or (2.4).

However, if a rule evolved in a situation where it always faced exactly the same pair of options (i.e. the same  $\theta$ ), then there would be no need for a rule that evaluates the times and amounts associated with the two choices: it would be enough to always choose the primed or unprimed option, whichever yields the highest fitness. Therefore, in analysing the fitness consequences of a rule, we must somehow specify the range of choice situations that the rule faces. We call this the *choice environment*. We assume that the choice environment is a list  $m$  of equally likely pairs of options (i.e.  $\theta$  values), so the average fitness that we seek to maximize is:

$$W(\rho_A, \rho_t) = \left( \sum_{i=1}^m W_{\theta_i}[p(\rho_A, \rho_t)] \right) / m. \quad (2.5)$$

In practice, we maximize the sum in the numerator because  $m$  is fixed for a given problem.

Next, we need to specify a choice environment that tests rules in a wide range of conditions. To begin, we consider a standard self-control situation with parameters  $\tau$  (inter-trial interval),  $t_s$  (delay to small),  $t_L$  (delay to large),  $A_s$  (small amount) and  $A_L$  (large amount). We can reduce the number of variables we must consider by rescaling. Thus, we scale temporal intervals by the delay-to-large  $t_b$  and amounts by the large amount  $A_L$  yielding three quantities  $\hat{\tau} = \tau / t_b$ ,  $\hat{t}_s = t_s / t_b$  and  $\hat{A}_s = A_s / A_L$ . This suggests a natural range of variation for  $\hat{t}_s$  and  $\hat{A}_s$ . Our numerical calculations allow  $\hat{t}_s$  and  $\hat{A}_s$  to vary over a grid of 100 equally spaced points in the square space defined by  $0 < \hat{t}_s < 1$  and  $0 < \hat{A}_s < 1$ . Since there is no such natural limit for the inter-trial interval  $\hat{\tau}$ , we simply consider a list of possible  $\hat{\tau}$  values (the  $\tau$  list) that combines factorially with the  $\hat{t}_s/\hat{A}_s$  grid.

Finally, we must convert these alternatives to our standardized choice notation, in a way that generates the same long-term consequences for the self-control and patch situations. Table 1 shows the transformations used to convert these alternatives into equivalent patch and self-control situations.

Table 1. Transformations used to create economically equivalent patch and self-control situations.

self-control		patch	
small immediate	large delayed	leave	stay
$t_1 = t_s$	$t'_1 = t_l$	$t_1 = \tau + t_s$	$t'_1 = t_l - t_s$
$A_1 = A_s$	$A'_1 = A_l$	$A_1 = A_s$	$A'_1 = A_l - A_s$
$t_2 = \tau$	$t'_2 = \tau$	$t_2 = 0$	$t'_2 = \tau + t_s$
$A_2 = 0$	$A'_2 = 0$	$A_2 = 0$	$A'_2 = A_s$

### 3. RESULTS

#### (a) Impulsive choice without discounting

Study 1 calculates the optimal  $\rho_A$  and  $\rho_t$  values without discounting. Our analysis is a numerical experiment with three factors: choice situation (self-control or patch), discrimination accuracy as measured by  $D$ , and the list of  $\tau$  values.

#### (i) Overview

Figure 3a shows a characteristic plot for study 1. The electronic Appendix A shows results for a broader range of conditions. For the patch situation, optimal  $\rho$  values are near zero, implying an impulsive choice rule, and discrimination accuracy has little effect on this result. In the self-control situation the optimal  $\rho_t$  approaches 1 when discrimination is very good (high  $D$ ), suggesting a rule that directly compares long-term rates; however, when discrimination is poor, optimal  $\rho_t$  values are small (impulsive) when  $\tau$  is small, and large (greater than one) when  $\tau$  is large. Note that  $\rho_A$  has no effect in the self-control situation (because  $A_2 = A'_2 = 0$  here).

A few caveats are required. First, the scale of plots required to show results for patch and self-control on the same graph can obscure effects of  $D$  in the patch situation; thus, while it is true that  $D$  has very little effect in the patch situation compared with its effect in self-control, it is not true that  $D$  has no effect in the patch situation. Second, although the optimal  $\rho$  values are near zero in the patch situation over the range we have studied, the behaviour of the optimal  $\rho$  values is more complex as  $D$  approaches perfect discrimination. When discrimination is perfect, all  $\rho$  values such that  $\rho_t = \rho_A$  give the same maximum long-term rate (electronic Appendix A). This generalizes the observation of Stephens & Anderson (2001) that the long-term ( $\rho_A = \rho_t = 1$ ) and short-term ( $\rho_A = \rho_t = 0$ ) rules are equivalent when discrimination is perfect in the patch situation.

The ecological rationality hypothesis claims that animals sometimes perform poorly in the self-control situation, because natural selection has equipped them with rules appropriate for the patch situation. We would like to investigate, therefore, the cost of implementing a ‘patch rule’ in a self-control situation. Figure 4 shows the cost of a patch-appropriate rule as a function of  $\hat{A}_s$  and  $\hat{t}_s$ . Figure 4 shows an elevated cost of using the patch-appropriate rule in self-control in a wedge-shaped region of the  $\hat{t}_s/\hat{A}_s$  space. The wedge corresponds to the region of  $\hat{t}_s/\hat{A}_s$  space where long- and short-term rules disagree, and as we would consequently expect, the wedge is narrow when  $\tau$  is small (since long- and short-term rules largely agree with  $\tau$  is small),

and broad when  $\tau$  is large. There is a striking peak in cost where  $\hat{t}_s$  and  $\hat{A}_s$  are both small; which is to say that an impulsive, patch-appropriate rule can do quite poorly when the small immediate alternative is very immediate and very small.

#### (b) The effect of discounting

The previous section shows how an interaction between choice context and imperfect discrimination can lead to the evolution of impulsive choice rules even when there is no discounting. Discounting is, however, a plausible feature of natural foraging. To address this issue, we repeated the analyses of the previous section using a fitness measure that incorporates a discount rate (equation (2.4)). With relatively minor modifications we repeated the analyses of the previous section at two levels of discounting (0.01 and  $0.1\text{ s}^{-1}$ ). If we assume that collection risk causes discounting, these discount rates correspond to averages of 0.6 and 6 collection-preventing interruptions per minute. While  $0.01\text{ s}^{-1}$  may be plausible, a loss in fitness of  $10\% \text{ s}^{-1}$  is absurdly large.

These levels of discounting change the results very little (figure 3b,c). The optimal value of  $\rho_t$  for the self-control situation decreases slightly as the discount rate increases as one would expect, but this effect is not large. The discount rate has almost no effect on optimal rules in the patch situation, presumably because these rules are already as impulsive as they can be. If we consider an extremely high level of discounting such as  $0.5\text{ s}^{-1}$ , we can create situations where optimal behaviour in self-control is ‘more impulsive’, but even here it is much less impulsive than behaviour appropriate for the patch situation. In effect, this observation repeats the claim we made in § 1 that absurdly high discount rates are required to account for observed behaviour, if we assume that fitness discounting *per se* explains animal impulsiveness.

A rather curious result occurs in the patch situation. We observed small increases in the parameter  $\rho_A$  when the discounting rate increased. This gives the paradoxical prediction that animals should value the second amount of food more when discount rates are high. This occurs, in our view, because the patch situation is a special case of the more general ‘foreground–background’-style choice problem. In the patch situation, the option with the more immediate food delivery (stay) is the only option with a second food delivery, so a rule that values the amount of the second food delivery will also favour the more immediate food delivery.

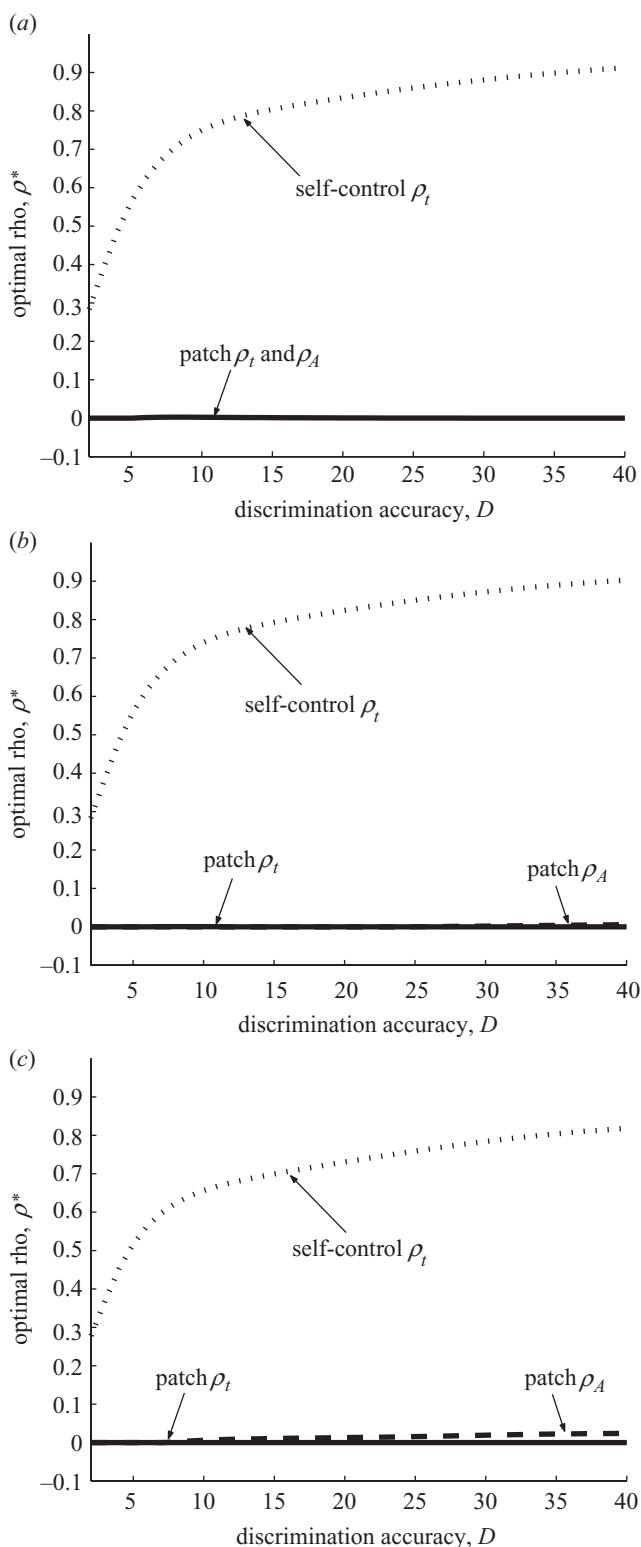


Figure 3. The figures show calculated optimal  $\rho$  values for patch and self-control situations for three different levels of discounting. (a) No discounting ( $\lambda = 0$ ), (b) a moderate level of discounting ( $\lambda = 0.01$ ), and (c) a very high level of discounting ( $\lambda = 0.1$ ). These calculations assume a discrete uniformly distributed list of  $\tau$  values with mean 3; specifically  $\tau \in \{0.1, 1, 3, 5, 9\}$ .

#### 4. DISCUSSION

Our model shows how natural selection can favour impulsive choice rules without temporal discounting. The struc-

ture of the patch situation reduces the long-term cost of impulsive rules. In addition, impulsive rules have a discrimination advantage over long-term rules, because ignoring common elements lets them evaluate a stronger signal of the relevant differences between a pair of alternatives. This leads to the surprising fact that an impulsive rule can achieve higher long-term rates of intake than a rule that actually compares long-term rates.

We find that optimal rules in the patch situation are impulsive regardless of discounting levels, and over a broad range of choice environments. By contrast, we find that optimal rules in the self-control situation vary widely. In a typical self-control situation, optimal rules are somewhat impulsive when discrimination is poor, and approach perfect far-sightedness as discrimination improves. However, we observed several other patterns in the self-control situation. We find that discounting increases impulsiveness in the self-control situation, but impulsiveness does not reach the extreme levels observed in the patch situation even when discount rates are absurdly large.

##### (a) Foreground–background

The patch situation is a special case of a more general choice situation that we call foreground–background choice. In these situations when a foraging animal encounters a feeding resource it must choose between (i) exploiting this resource and then returning to its normal ‘background’ strategy, or (ii) ignoring the resource and continuing with its background strategy. We call the encountered resource the foreground option to contrast it with the background. We argue that in many natural choice situations an animal’s alternatives take the form ‘background versus foreground then background’. These choices are not strictly mutually exclusive as in laboratory studies; instead, the ‘background’ is part of both alternatives. The animal does not forgo the background option when it chooses to exploit the foreground option. The patch situation is a simple foreground–background situation, because the leave option is in the background of both alternatives. In combination with plausible constraints on the accuracy of discrimination, foreground–background choice can be a powerful force favouring the evolution of impulsivity.

##### (b) What is discounting?

Students of impulsivity use the word ‘discounting’ in several different ways, and the reader should understand these differences to avoid confusion. Explanations of the evolution of impulsivity have invariably focused on how delay discounts the fitness value of food reward, typically invoking collection risk or life-history effects (e.g. Kagel *et al.* 1986; McNamara & Houston 1987; Benson & Stephens 1996; Green & Myerson 1996; Sozou 1998). We will call this *economic discounting*, and clearly it is something that is external to the animal. The use of economic discounting to explain impulsivity is so entrenched that investigators often use ‘discounting’ as a synonym for impulsiveness. When used in this way the word discounting has no particular connection to lost value, but simply means that delay strongly affects observed preference. Psychologists, for example, have carefully documented ‘discounting’ functions that describe the relationship between delay and preference (e.g. Mazur 1987, 1997, 2001). Some psychologists seem to take this logic a step further

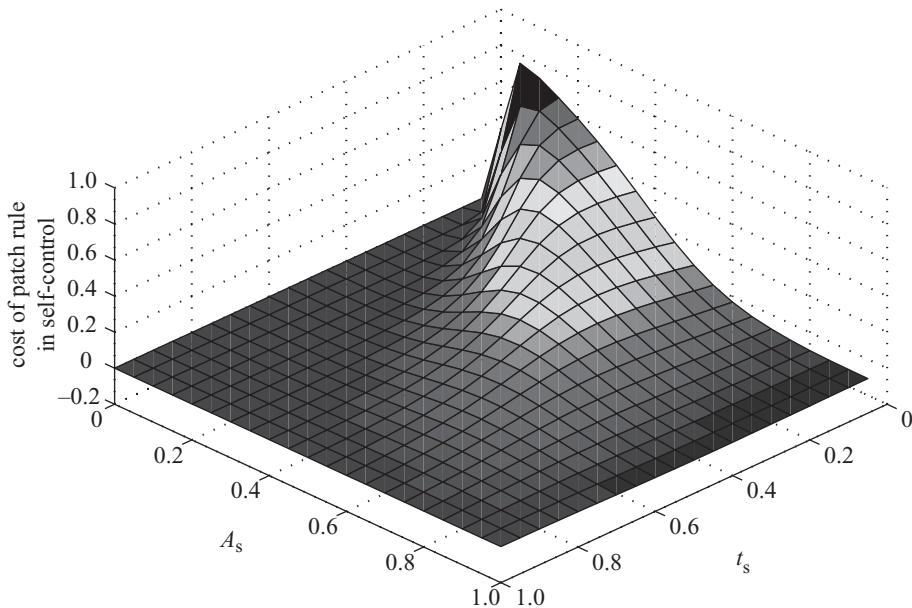


Figure 4. The cost of implementing a patch-appropriate rule in a range of self-control situations for a range of normalized  $t_s$  (delay to small;  $1 > t_s > 0$ ), and  $A_s$  (amount of small;  $1 > A_s > 0$ ). This plot shows the cost of implementing a patch rule for a specific pair of self-control alternatives. There is a roughly triangular region where it is costly to implement a patch rule in the self-control situation. This plot assumes  $\tau = 5$  and  $D = 5$ . Notice that there is a large region where it is not costly to use the ‘wrong rule’. Thus, while experimentalists can arrange situations where patch-appropriate rules do poorly, overall patch-appropriate rules are fairly robust.

(although they seldom state this explicitly) by suggesting that impulsive animals possess an internal discounting mechanism that reduces their subjective assessments of delayed food rewards. We call this *subjective discounting*. Our model shows that we do not need economic discounting to explain the evolution of impulsiveness. Nothing about our model excludes the possibility that subjective discounting plays a role in the proximate mechanism of impulsiveness.

The phrase ‘ecological rationality’ applies to our approach because we argue that natural selection should favour impulsive choice rules in a specific, common ecological situation. That is, we claim that impulsivity is rational in the limited context of foreground–background situations, even though it is not a good mechanism for arbitrary choice problems. The name ecological rationality hypothesis does not suggest that other explanations of impulsiveness lead to irrational behaviour.

### (c) Related models and limitations

The significance of our work depends on levels of discounting. If natural selection has evaluated food gains in a way that strongly devalues delayed rewards, then one might argue that this alternative to discounting is unnecessary. Behavioural ecologists interested in impulsiveness have tended to focus on explaining the form of discounting (hyperbolic versus exponential) rather than its magnitude (Bateson & Kacelnik 1996; Green & Myerson 1996; Sozou 1998), and so we have only rather vague claims about expected levels of discounting. We argue that the effects of delay on fitness (discount rates) will be too small to explain observed levels of animal impulsiveness. Relatively simple calculations suggest that we need initial discount rates of between 1% and 50%  $s^{-1}$  to explain non-human impulsiveness. By contrast, economists (Weitzman 2001) offer

first-principles estimates for human discounting of ca. 4% per year, or  $1.2 \times 10^{-7} s^{-1}$ !

Previous evolutionary explanations of impulsiveness focus on economic discounting in one form or another. For example, a relatively small number of authors (Rogers 1994; Sozou & Seymour 2003) develop life-history-style explanations that derive discount rates from mortality and fecundity schedules. In this approach, impulsiveness occurs because more immediate rewards lead to more offspring; while this is undoubtedly correct and important, it seems unlikely to explain impulsive choice in the range of seconds or even tens of seconds. Most modellers have focused on discounting by interruptions (e.g. Kagel *et al.* 1986; McNamara & Houston 1987; Benson & Stephens 1996; Green & Myerson 1996; Sozou 1998). This is the a-bird-in-the-hand-is-worth-two-in-the-bush idea: delayed rewards are worth less because some ‘interruption’ might prevent an animal from collecting a delayed reward. There are many of these ‘discounting by interruptions’ style models ranging from simple to quite complex. Sozou (1998) presents the most sophisticated and creative of these models.

Among psychological approaches, Mazur’s development of the hyperbolic model and the supporting experimental studies stands out as especially relevant and insightful. The hyperbolic model has several key properties that agree with the observations. Notably, it correctly predicts that impulsivity decreases with delay. Our rules have this property (as do all rate-based models). Many explanatory models, whether based on life-history parameters or interruptions, have sought to explain the hyperbolic or decreasing ‘discount’ rate properties of observed preferences (e.g. Sozou 1998; Stephens 2002). By contrast, we have focused on the intensity of impulsiveness.

Our patch situation is only a simple foreground–background situation, and this could limit the generality of our

results. In addition, we selected the  $\rho$ -form of our rules for our convenience. It would be instructive to use rules and parameters derived from more biologically motivated models of choice mechanisms, such as neural networks or signal-detection theory. In addition, one can imagine choice situations that are more complex in many ways. For example, we are currently exploring the effect of options that vary stochastically.

We offer a new explanation of animal impulsiveness, based on ecological rationality rather than temporal discounting. We show that impulsive decision mechanisms can evolve without discounting. Indeed, it is simple to find situations where short-sighted rules lead to higher long-term rates of intake than rules that directly compare long-term rates. Our hypothesis has two basic components: (i) the foreground–background structure of naturally occurring choices reduces the long-term costs of impulsiveness, and (ii) impulsive rules have an advantage in a world of imperfect discrimination, because they compare shorter temporal elements: they achieve more accurate discrimination. Our hypothesis offers a strong and plausible alternative to the long-standing dominance of discounting explanations of impulsiveness.

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